

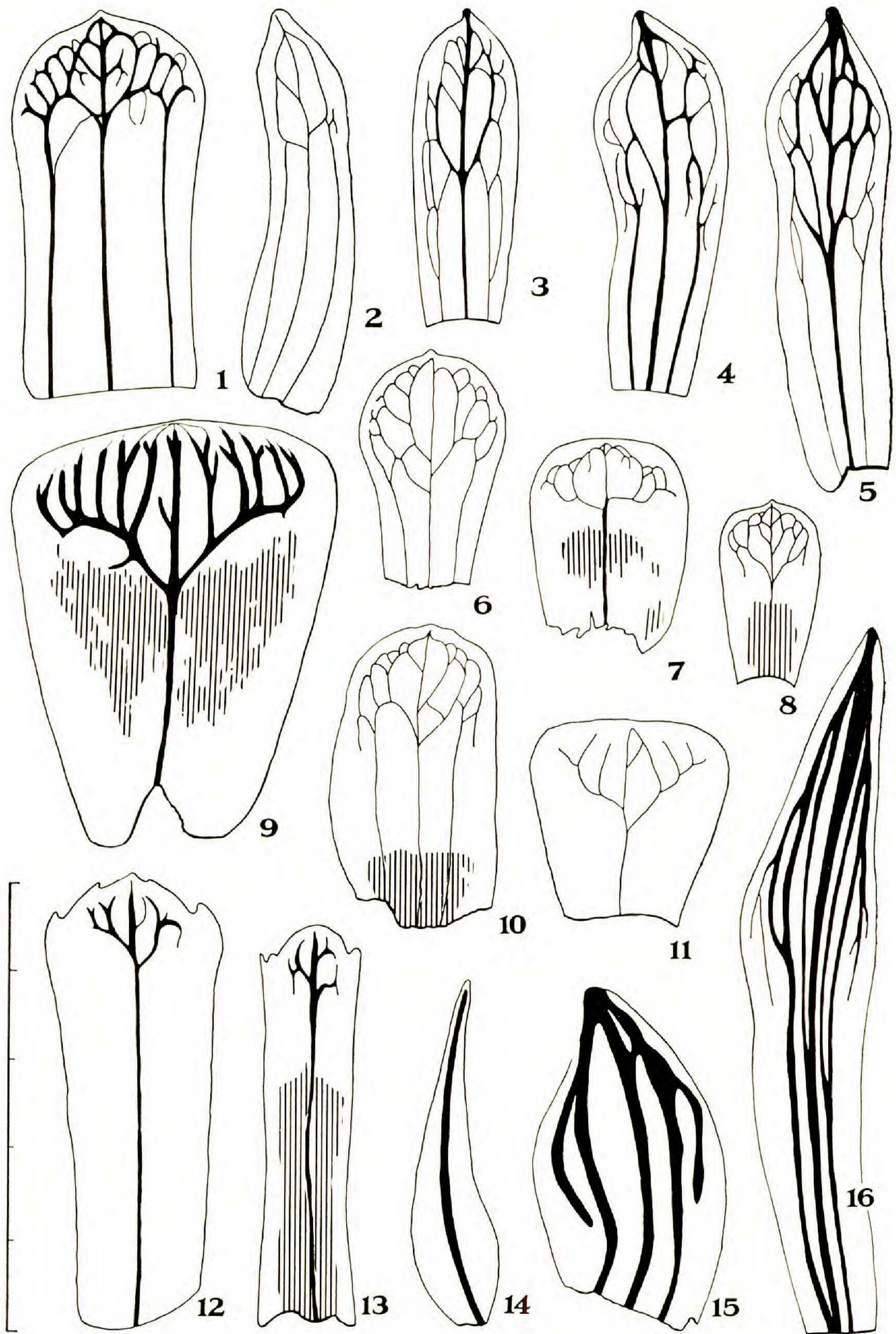
LEAF VENATION AND PUBESCENCE IN THE
GENUS RAOULIA (COMPOSITAE)

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MODERN DICOTYLEDONS are characterized by a highly diversified pattern of reticulate foliar venation, and true open venation is a rare occurrence. The persistence of presumably primitive dichotomous open venation in *Kingdonia* (Ranunculaceae?) and *Circaeaster* (Ranunculaceae?, Circaeasteraceae?) as shown recently by Foster (1959a,b) suggests that reticulate venation has probably evolved from dichotomous venation. On the other hand, species of the genus *Raoulia* provide an example of an "open" venation which is derived, rather than primitive. Since the venation of *Raoulia* has not been studied in detail previously, the present investigation is an attempt to provide further data which may contribute both toward a better understanding of the complicated picture of venation in angiosperms and toward a more natural classification of the genus *Raoulia* itself.

Raoulia comprises a group of specialized plants which are typically found in dry, rocky habitats between sea level and 2000 meters in both the North and South Islands of New Zealand (to which the genus is restricted, with one possible exception in New Guinea). The habit varies from small, compact, creeping or tufted herbs to small or large cushion-forming plants of the type commonly known as "vegetable sheep." The genus belongs to the family Compositae, tribe Inuleae, subtribe Gnaphaliinae, a taxonomically difficult subtribe in which limits of genera are not always very clear. Within the group *Raoulia* is, in fact, defined as much by its habit and geographical distribution as by any qualitative character (Cheeseman, 1925). As treated by both Beauverd (1910, 1912) and Cheeseman (1925), the genus is composed of 21 species grouped into two subgenera. These are further divided into two and three sections respectively, according to involucre and foliar characters. Material of seventeen species including representatives of each of the sections has been available for study. In the discussion which follows the nomenclature is that of Beauverd.

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FIGS. 1-16. Leaf venation of species of *Raoulia*. Veins in black, mesophyll sclereids in longitudinal hatching. Differences in width of veins due to sclerenchyma. Each division of scale = 1 mm. 1, *Raoulia Petriensis* Kirk (*Cheeseman s.n.*, GH); 2, *R. glabra* Hook. f. (*Cheeseman s.n.*, GH); 3, *R. subsericea* Hook. f. (*Petrie 193*, GH). 4, *R. tenuicaulis* Hook. f. (*Kirk s.n.*, GH); 5, *R. Monroi*

MATERIAL AND METHODS

Most observations were made from dried herbarium specimens, for only two species, *Raoulia glabra* and *R. australis*, could be studied from living material. The leaves, bracts and flowers of all available species of *Raoulia* were cleared according to the technique of Foster (1955; see also Arnott 1959). In order to extract some dark material which remained after treatment with sodium hydroxide and chloral hydrate, leaves were bleached in a 50% solution of "Clorox" until reasonably clear, usually about five minutes, and then thoroughly washed to assure good subsequent staining. The leaves and stems of certain species of *Raoulia*, especially the cushion-forming ones, are heavily impregnated with tannins and other dark-staining substances. In order to remove these, long treatment with sodium hydroxide and "Clorox" is needed which damages the leaves or makes them so brittle that they disintegrate when the heavy coat of hairs is removed. Therefore, the clearing process often had to be interrupted as soon as a reasonably good view of the venation was obtained.

Both surfaces of the leaves of all species of *Raoulia* are covered with a thick layer of long trichomes which entirely cover the leaf and which it was necessary to remove in order to study the venation. This was done by "shaving" the hairs off with a sharp scalpel after the leaves had been cleared and dehydrated. The smallness of the leaves (less than one centimeter in every case) and their fragility made this operation a tedious, time-consuming, and "nerve-shattering" operation and resulted, in spite of extreme care, in a high degree of tearing of the leaves.

OBSERVATIONS AND RESULTS

Leaf shape. The leaves of all species of *Raoulia* are small. The size of the mature leaves varies from 3 mm. in leaves of *R. lutescens* and *R. Goyenii* to nearly 8 mm. in *R. grandiflora*. Most species have leaves of 4–5 mm. in length.

In general, the leaves are appressed to the shoots. The degree to which they are appressed varies greatly and is correlated with the general habit of the plant. In such creeping species as *R. glabra* or tufted ones as *R. grandiflora*, the leaves are appressed to the shoot only at their bases and are curved outward above. In these cases the leaves are somewhat keeled and divergent. The leaves of these species are generally broadly linear-lanceolate or subulate and are usually longer than the average for the genus.

Hook. f. (*Kirk s.n.*, GH); 6, *R. Parkii* Buchanan (*Anderson 171*, GH); 7, *R. bryoides* Hook. f. (*Cheeseman*, 1911 GH); 8, *R. lutescens* Beauverd (*Anderson 106*, GH); 9, *R. Buchananii* Kirk (*Cockayne 7041*, A); 10, *R. australis* Hook. f. (*Kirk s.n.*, GH); 11, *R. Goyenii* Kirk (*Kirk s.n.*, GH); 12, *R. eximia* Hook. f. (*Cockayne 7048*, GH); 13, *R. mammillaris* Hook. f. (*Kirk s.n.*, GH); 14, *R. subulata* Hook. f. (*Petrie 149*, GH); 15, *R. Hectorii* Hook. f. (*Petrie 203*, GH); 16, *R. grandiflora* Hook. f. (*Petrie*, 1889, GH).

On the other hand, in the cushion-forming species, such as *R. bryoides* or *R. rubra*, the leaves are very much crowded in a tightly appressed spiral, with the lower leaves covering most of the outer surface of those lying above. The leaves are rather flat, not keeled, and usually rectangular or nearly rectangular in shape.

Aside from these two types, there are some intermediate ones, which are correlated with intermediate habit of growth (see TABLE I).

Venation. Three main types of venation can be distinguished in *Raoulia*: the reticulate type (I), with three main veins; the semireticulate (II), with either three or more frequently one main vein; and the striate type (III).

I. **RETICULATE TYPE.** The basic type is represented by *Raoulia Parkii* (FIG. 6). Three main veins enter the leaf base from the stem. The mid-vein branches two or three times and these branches in turn form lateral branches which anastomose with the two lateral veins, forming a simple reticulum. The following species can be arranged in a progressively simpler series. In *R. tenuicaulis* (FIG. 4) some of the secondaries do not connect and the leaf presents a "semiopen" pattern. *Raoulia Monroi* (FIG. 5) is very similar in venation to *R. tenuicaulis*. In *R. subsericea* (FIG. 3), the reduction is a little more accentuated: the laterals are less well marked, and the connections between the central and the lateral veins are usually unbranched. Some lateral open veinlets occur in this species. Finally, in *R. glabra* (FIG. 2) there are a main and two lateral veins with three to four connecting veins, and an occasional freely terminating veinlet. The pattern in *R. glabra* is scarcely reticulate.

II. **SEMIRETICULATE TYPE.** This type is not so clearly delimited as the preceding one, and, although a linear reduction series can be inferred, a subdivision into loosely connected subgroups (indicated by the letters a, b, c, and d) is probably more significant.

a. *Raoulia australis* (FIG. 10) and *R. Petriensis* (FIG. 1) have three main veins, which run unbranched for about three-fourths of the length of the leaves. These veins then branch forming a coarse meshwork with some unconnected veinlets. In *R. australis* the secondaries are relatively fewer than in *R. Petriensis*. These two species are the only ones of this type with three main veins and form a link with the plants of the preceding type, particularly with *R. Parkii*, from which the leaves do not differ greatly.

b. *Raoulia lutescens* (FIG. 8) and *R. bryoides* (FIG. 7) have basically the same or a similar arrangement of the end veinlets as *R. australis*, but, instead of three main veins, they only have a midvein running the length of the leaf. Two open veinlets which point towards the base of the leaf at each side, of the terminal reticulum seem to indicate arrested stages in the development of the two lateral veins, a situation similar to that in *Minuartia aretioides* (Caryophyllaceae) (Troll 1938, pp. 1085, 1086). Whether these veins have disappeared through reduction, or whether this is an indication of a first stage in development, cannot be answered with

certainty. However, the increasing specialization in other features of the plant, correlated with the simple leaf venation in this type, indicates that a reduction series is the more likely possibility.

c. *Raoulia Buchananii* (FIG. 9), *R. Goyenii* (FIG. 11), and *R. rubra* (FIG. 24), in this order, show an increasing simplification in the pattern described in the above paragraph. The noteworthy features here are that there is no indication of vestigial lateral traces, and that the ultimate veinlets are dichotomously branched and terminate freely without anastomosing. The maximum degree of simplification is evident in *R. rubra*.

d. *Raoulia mammillaris* (FIG. 13) and *R. eximia* (FIG. 12) also have an extremely simple venation which consists in these species of the midvein and, toward the tip of the leaf, two or three secondaries, which may or may not bifurcate in turn. A very interesting feature is that the midvein and the secondaries are very oddly shaped and enclosed by a sheath of sclereids.

III. STRIATE TYPE. Three species are of this type which is apparently not connected with the other two types. *Raoulia grandiflora* (FIG. 16) has the most elaborately developed venation of the three species. Three main veins enter the leaf. (Sometimes two of them are anastomosed at the very base of the leaf. Whether this indicates a possible one-trace condition at the node is not known.) The midvein bifurcates once or twice, the branches running parallel and finally anastomosing with the lateral veins towards the tip of the leaf. The lateral veins sometimes bifurcate, the branches of this division running parallel and then uniting again to form an elliptical loop. All three main veins meet at the tip of the leaf. One or more backward-pointing open veinlets are usually present at each side of the lateral veins. Short strands of vascular tissue unconnected with the system of veins are sometimes present. In *R. Hectorii* (FIG. 15) the pattern is essentially the same but much reduced, since usually neither the midvein nor the lateral veins branch. In *R. subulata* (FIG. 14) there is only a single unbranched midvein, the laterals having disappeared. The unique feature, aside from the venation, which unites these three species, is the extreme width of the vascular bundles which are covered by a thick sheath of sclereids.

Sclerenchyma. The leaves of *Raoulia* present always a strong development of sclereids. This is more evident in the older leaves, in which may also be found parenchyma cells (and even epidermal cells) with thickened, lignified walls and forming a sheet that can occupy up to two-thirds of the leaf surface.

The development of sclerenchyma fibers surrounding the vascular bundles varies from species to species. In *R. glabra* there is a relatively small development, but sclerenchyma usually forms an enveloping sheath at least as thick as the bundle proper. In the species with a striate type of venation (*R. grandiflora*, *R. Hectorii* and *R. subulata*) the develop-

ment of a sheath of sclerenchyma fibers around the bundles is particularly notable (Figs. 14–16). Still, in other species, such as *R. Buchananii*, *R. eximia*, and *R. mammillaris* irregularly shaped sclereids are associated with the vascular bundles, particularly towards the end of the veins (Figs. 9, 12, 13). These sclereids account for the irregular diameter and shape of the bundles. In some species with “open” venation (e.g., *R. Buchananii*) the tip of the bundles may be totally devoid of sclereids.

Sclereids are also present sometimes in the mesophyll. In these cases they are elongated polygonal cells with thickened walls. They are particularly prominent in *R. Petriensis*, *R. bryoides*, and *R. Buchananii* (Figs. 1, 7, 9), where they are present in very young leaves. Nevertheless, in most species some mesophyll sclereids are present, particularly in older leaves.

Mesophyll sclereids usually form a broad sheet at each side of the midvein in the lower and middle portion of the leaf. They may also be present in isolated groups or forming small patches. The exact position of these sclereids is unpredictable in any particular leaf, but they are never present in the upper fourth of the lamina.

Trichomes. As already mentioned, the surface of the leaves is covered by a thick cap of trichomes. These are long, uniseriate, multicellular hairs, of a type occurring commonly in Compositae (Metcalf and Chalk, 1950). The type of hair is the same in all species, but there are differences in the general appearance and distribution of hairs on the leaf surface. The genus can be divided into two groups of species: 1) those which have their leaves covered by a thick layer of tightly interwoven trichomes forming a felt-like cap; 2) those that have their leaves with a cover of more or less straight and somewhat stiff hairs that usually point towards the apex of the leaves. Finally, *Raoulia subulata* has glabrous leaves, whereas *R. glabra* has only a few and widely spaced hairs on the leaf surfaces. Species of the first type usually have the entire leaf surface covered with a thick cap of interwoven hairs which may be as thick as or thicker than the leaf tissues proper. On the other hand, the species which have hairs of the “stiff” type, have these concentrated on the apical end and usually more densely on the adaxial surface in this region. These differences can be correlated with the pattern of apical growth. The species with “interwoven” hairs have more elongated stems and reflexed leaves. On the other hand, the species with “stiff” hairs are true cushion plants. Their cauline leaves are numerous, imbricated, and closely appressed. As a consequence, only the upper third of the leaf is exposed.

DISCUSSION

Raoulia leaves present some of the few instances of open venation in dicotyledonous angiosperms. Although an open dichotomous venation is considered primitive in gymnosperms and vascular cryptogams, this con-

dition is undoubtedly secondary and derived in *Raoulia*, as already pointed out by Troll (1938).

That this is so can be inferred from two sets of facts: 1) the correlation of open venation with specialization in other features of the plant; 2) the entirely different typology of the venation of *Raoulia* and of a typically primitive dichotomous venation as found in some gymnosperms and vascular cryptogams or in the primitive angiosperm *Kingdonia uniflora* (Foster 1959b). Further evidence is to be found in the venation of *Ewartia*, undoubtedly the genus closest to *Raoulia* (Beauverd 1910). The venation of both species of *Ewartia* investigated, *E. catipes* (FIG. 26) and *E. nubigena* (FIG. 25), is reticulate and of a type similar to that of *Raoulia Parkii*, although more elaborate. Since other *Gnaphaliinae*, including *Gnaphalium* itself, have a venation along the same lines as that of *Ewartia*, it may be concluded that the venation of *Raoulia* is atypical and specialized.

At this point it may be of interest to see how the venation of *Raoulia* compares with that of *Kingdonia uniflora*, believed to be truly primitive (Foster 1959b). The nodal anatomy of *Raoulia* is not known, but the vascular supply of the leaf is formed by one to three traces. *Kingdonia* has a unilacunar node, with four bundles (two of which may appear as double strands) forming the vascular supply of the foliage leaf. More significant still is the total venation pattern. The veins in *Kingdonia* are dichotomously branched, the forks of the branches extending usually into the tips of the dentations. Occasional anastomoses, as well as "blind" endings unrelated to the dentations are not uncommon, but in general the pattern is quite regular and symmetric. In contrast with this, the pattern in *Raoulia*, even in those species with a very simple and "open" venation (e.g., *R. eximia* or *R. rubra*), is irregular, and of a type altogether different. While *Kingdonia* has a dichotomous venation, *Raoulia* has a branching pattern which does not follow any regular established system. This is probably due to the connection of the "open" venation of *Raoulia* with the extreme reduction in the lamina and its derivation from a reticulate type. The "open" situation when present is possibly the result of arrested growth of the veinlets. In contrast, the regularity of the "open" venation in *Kingdonia* is the consequence of the full development of the leaf along an established pattern.

It is interesting to note that in *Kingdonia* and in at least one species of *Raoulia* (*R. grandiflora*) short strands of vascular tissue unconnected with the system of veins are found. The reason for this remains unexplained. The position of these strands and their occurrence are rather erratic in both species.

In brief we may say that, notwithstanding the fact that the types of venation present in *Raoulia* and *Kingdonia* have been sometimes classed together (Troll 1938), careful analysis reveals that they are very different. Not only is one clearly derived and the other probably primitive, but there are also differences in number of traces, branching pattern, and

regularity of veinlets. This once more demonstrates the necessity for a detailed study of the totality of the venation in angiospermous leaves, as has been repeatedly emphasized by Foster (1950, 1952, 1959b).

From the morphological and anatomical point of view, the unique overall pattern of venation in *Raoulia* is of interest. No other group of species so far investigated shows a similar venation pattern.

The question of what determines the particular pattern of a leaf has occupied the attention of various workers, most of whom have tended to correlate "distribution of growth" with venation pattern. The corresponding bibliography has been reviewed critically by Foster (1952). The main conclusions which Foster draws from the literature are: 1) "that the 'distribution of growth' appears to vary widely in leaves, even between ones which are similar in form at maturity" and 2) "that the course of the main veins of the lamina 'registers' more or less faithfully the distribution of the longitudinal and transverse growth which occurred during ontogeny." Foster's own studies on *Quiina pteridophylla* show that this interpretation is rather "naive" and that intensive ontogenetic and comparative studies are needed before any major conclusion can be drawn. A similar conclusion is reached by Pray (1954) as a result of his studies on *Liriodendron*.

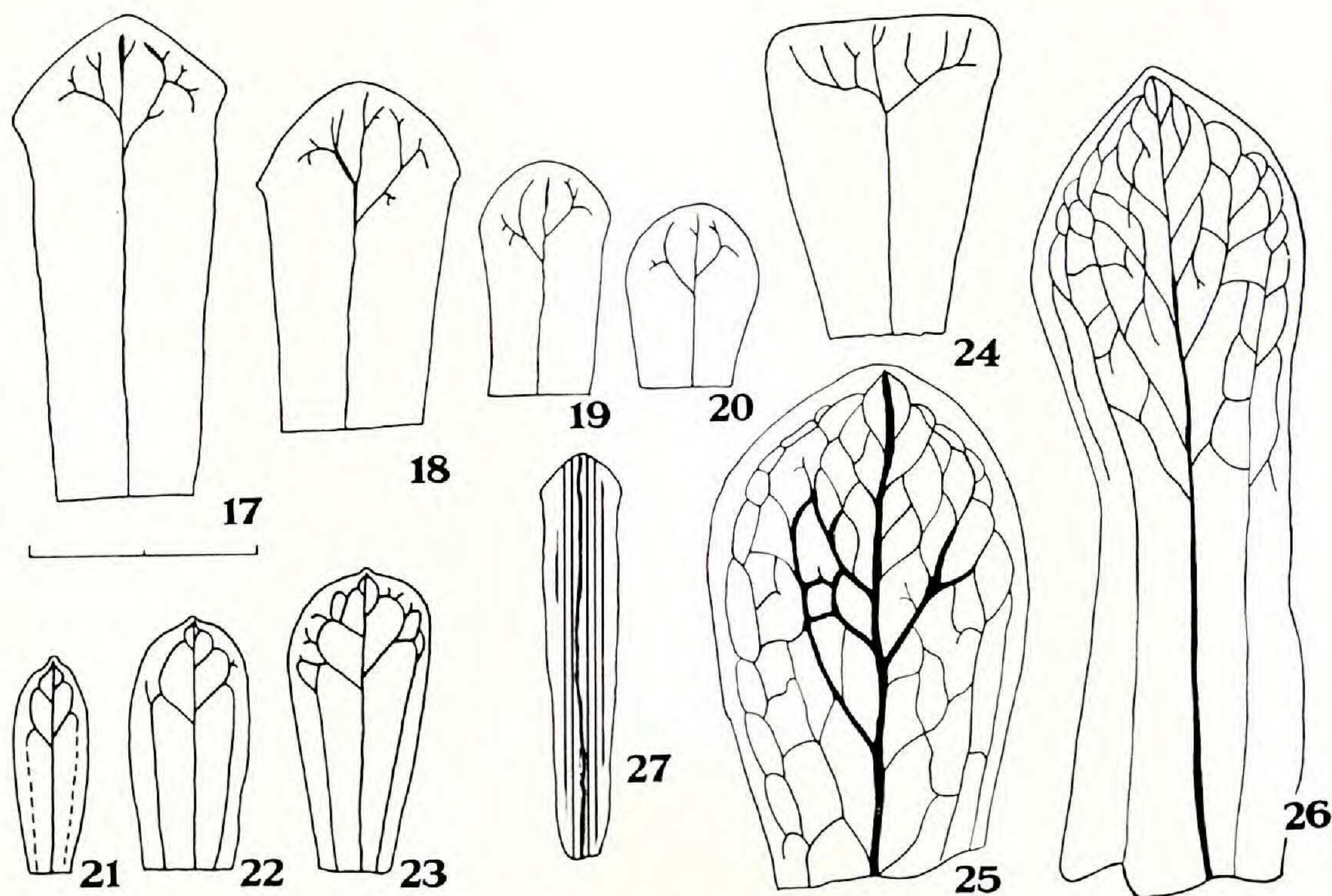
No juvenile material was available for this study, and the extremely small size of the leaves and their heavy coat of hairs militated against the successful examination of leaf primordia. Also, lack of fresh material and of sufficient dried herbarium material of critical species precluded the use of sections. Nevertheless, the few data obtained seem to indicate that the venation pattern is influenced by — among other causes, undoubtedly — the pattern of growth of the leaf, which is, in turn, determined to some degree by the general organography of the shoot.

In FIGURES 17–20 are depicted four successively smaller primordia of *Raoulia eximia* and in FIGURES 23–21 similar stages in leaves of *R. Petriensis*. Growth in width apparently takes place very early, while the primordium is very small (less than 2 mm.). At that time the pattern of the end "reticulum" is laid down and later growth in length has no important effect on it. A full interpretation will have to wait until more physiological and ontogenetical studies have been completed.

In brief, the venation types of *Raoulia* seem to be associated with the habit of the plant and the growth pattern characteristic of it. Simple venation types are correlated with extreme adaptive modification in other structures. A similar conclusion with respect to the node has already been pointed out by Bailey and Nast (1944).

It may be significant that the venation pattern of the leaves of *Raoulia* is similar to that found sometimes in involucre and receptacular bracts of other Compositae. Müller (1938) has made an extensive study of venation patterns in various types of phyllomes. She regards cataphylls, bracts, and perianth members as reduced structures corresponding to the bases of foliage leaves. Her evidence is the overall similarity of venation patterns in the various phyllomes in spite of differences in the nodal anatomy.

Post (1958) finds a similar situation in his investigations on the genera *Frasera* and *Swertia* (Gentianaceae). It might therefore be better from the morphological point of view to classify the foliage leaves of *Raoulia* as bracts, even though they carry the bulk of the photosynthetic activity. This points once more to the difficulty in defining the different types of phyllomes. The venation pattern in the involucral bracts of *Raoulia*, on the other hand, is similar in all species, consisting of a single vein which runs unbranched the entire length of the bracts (FIG. 27).



FIGS. 17-24. Leaf venation of species of *Raoulia*. Veins in black, differences in width due to sclerenchyma. Each division of scale = 1 mm. 17-20, Leaf primordia of *R. eximia* Hook. f. (Cockayne 7048, GH); 21-23, Leaf primordia of *R. Petriensis* Kirk (Cheeseman s.n., GH); 24, *R. rubra* Buchanan (Cranwell, 1933, UC). FIGS. 25-26. Leaf venation of species of *Ewartia*. Veins in black, differences in width due to sclerenchyma. 25, *E. catipes* Beauverd (Hooker, 1839-43, GH); 26, *E. nubigena* Beauverd (Von Müller s.n., GH). FIG. 27. Involucral bract of *Raoulia lutescens* Beauverd (Anderson 106, GH), showing midvein and sclerenchyma (hatching).

Finally, one should mention the probable application of the results of these investigations to the taxonomy of the group. TABLE I shows various characteristics of the species here considered.

The genus was divided by Beauverd (1912) into two subgenera, *Raoulia* (*Eu-Raoulia*) and *Psychrophyton*. This division, based mainly on characters of the pappus and number of flowers, is substantiated by the results of this study as far as the species here investigated are concerned. Subgenus *Raoulia* is composed of compact, semicreeping plants which grow between sea level and 1800 m. altitude. The leaves are lanceolate to oblong-lanceolate in shape. All species but one, *R. lutescens*, have three traces

forming the vascular supply to the foliage leaf. The venation is either of the reticulate type or of the semireticulate type, but no species with "open" venation belongs to this subgenus. The pubescence is of the "interwoven" type, with exception of *R. glabra* which has very few hairs.

Most members of subg. *Psychrophyton* are true cushion plants from

TABLE I. Characteristics of species of *Raoulia*.

SPECIES	HABIT	ALTITUDINAL		PUBESCENCE TYPE	MAIN VEINS	VENA- TION TYPE
		RANGE (meters)	LEAF SHAPE			
Subg. <i>RAOULIA</i>						
<i>Parkii</i>	semicreeper	750-1800	lanceolate	interwoven	3	I
<i>tenuicaulis</i>	semicreeper	0-1650	lanceolate	interwoven	3	I
<i>Monroi</i>	semicreeper	0-1150	lanceolate	interwoven	3	I
<i>subsericea</i>	semicreeper	300-1600	lanceolate	interwoven	3	I
<i>glabra</i>	semicreeper	0-1500	lanceolate	semiglabrous	3	I
<i>australis</i>	semicreeper	0-1600	lance-oblong	interwoven	3	IIa
<i>Petriensis</i>	semicreeper	1500	lance-oblong	interwoven	3	IIa
<i>lutescens</i>	semicreeper	300-1800	lance-oblong	interwoven	1	IIb
Subg. <i>PSYCHROPHYTON</i>						
<i>bryoides</i>	cushion	1200-2100	oblong	straight	1	IIb
<i>eximia</i>	cushion	1350-2000	oblong	straight	1	IIc
<i>mammillaris</i>	cushion	1300-2000	oblong	straight	1	IIc
<i>Buchananii</i>	cushion	1200-1600	oblong	straight	1	IIc
<i>Goyenii</i>	cushion	400-1500	oblong	straight	1	IIc
<i>rubra</i>	cushion	1500	oblong	straight	1	IIc
<i>grandiflora</i>	tufted	1000-1800	lance-subulate	interwoven	3	III
<i>Hectorii</i>	tufted	1200-1800	subulate	interwoven	3	III
<i>subulata</i>	tufted	1200-2000	subulate	glabrous	1	III

higher altitudes, usually above 1000 m., although *R. Goyenii* can be found at lower altitudes. *R. grandiflora*, *R. Hectorii* and *R. subulata* form small tufts, rather than appressed cushions. The leaf shape of species in subg. *Psychrophyton* is either oblong or subulate. The pubescence type is either straight, in the true cushion plants, or interwoven, in *R. grandiflora*, *R. Hectorii*, and *R. subulata*. These last three species have a striate venation, while the rest of the species of this subgenus investigated have a semireticulate venation with only one trace entering the leaf from the node.

Subgenus *Psychrophyton* was divided by Beauverd (1912) into three sections: *Uninerves*, those species with only one trace entering the leaf and a nontruncate leaf apex; *Truncatae*, species with truncate leaf apices, and *Trinerves*, species with three traces entering the leaf. As can be seen from the data of TABLE I, this is an artificial division. A more natural arrangement is to divide the subgenus into two groups: one including *R. grandiflora*, *R. Hectorii* and *R. subulata*, which share the tufted habit, the subulate or subulate-lanceolate leaves, the interwoven type of pubescence, and the striate venation; the other group comprising the cushion plants with oblong leaves, "straight" pubescence, and the semireticulate type of venation.

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